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Contrasting Patterns of Genetic Diversity in European Mammals in the Context of Glacial Refugia

Oxala García-Rodríguez [1,*](ID), Emilie A. Hardouin [1](ID), Debbi Pedreschi [2](ID), Martin B. Richards [3](ID), Richard Stafford [1](ID), Jeremy B. Searle [4,†](ID) and John R. Stewart [1,†](ID)

1   Department of Life and Environmental Science, Faculty of Science and Technology, Bournemouth University, Christchurch House, Talbot Campus, Poole, Dorset BH12 5BB, UK; ehardouin@bournemouth.ac.uk (E.A.H.); rstafford@bournemouth.ac.uk (R.S.); jstewart@bournemouth.ac.uk (J.R.S.)
2   Marine Institute, Oranmore, Co., H91 R673 Galway, Ireland; debbi.pedreschi@marine.ie
3   School of Applied Sciences, University of Huddersfield, Queensgate, Huddersfield HD1 3DH, UK; m.b.richards@hud.ac.uk
4   Department of Ecology and Evolutionary Biology, Corson Hall, Cornell University, Ithaca, NY 14853, USA; jeremy.searle@cornell.edu
*   Correspondence: oxalagar@gmail.com
†   These authors contributed equally to this work.

Abstract: Phylogeographic studies have been conducted on many different mammal species in order to track their recent demographic histories. The climatic fluctuations associated with the Last Glacial Maximum (LGM) appear to have had a profound influence on the geographic patterning of genetic diversity in mammals. However, most phylogenetic studies have focused on single species. Few have used a holistic approach covering multiple taxa to explore common patterns. Here, we conducted meta-analyses of mitochondrial DNA control region sequences, identifying haplotype diversity and private allelic richness patterns in a geographic context. Four general patterns emerged among European mammals: an east–west decline in variation, a Western-Central belt of the highest diversity, southern richness, and homogeneity with no geographic pattern. These patterns likely reflect the refugial origins of modern populations. The east–west variation decline suggests species with eastern LGM refugia; the Western-Central belt of the highest diversity may harbor taxa with cryptic northern refugia, while southern richness may correspond to traditional southern refugia. Species with homogeneity and no geographic pattern may have been panmictic without a specific refugium or may reflect the occurrence of both southern and cryptic northern refugia. Surprisingly, the "no pattern" phenomenon is seldom discussed and may frequently have been discounted. Our study emphasizes the importance of considering multiple taxa, providing valuable insights into the responses of European mammals to past climatic changes.

Keywords: phylogeography; mitochondrial DNA; mammals; last glacial maximum; meta-analysis

1. Introduction

In the last three decades, phylogeography has become a major component of biogeography at the within-species level and has helped understand the shaping of contemporary geographic patterning of genetic lineages by climate change during the Pleistocene [1,2]. During glacial periods, the distributions of temperate and cold-adapted species contracted or expanded due to their climate adaptations [3–9]. Those areas representing the species' maximum contraction in a geographical range are called refugia [7,10]. The last glacial maximum (LGM), 24,000 to 15,000 years ago, has been of particular importance in shaping the genetic landscape of many species [11].

The data presented in the first phylogeographic studies of Europe suggested that the majority of temperate species analyzed responded with end-glacial/post-glacial colonization of central and northern Europe from southern refugia [3,12–14]. These southern

refugia have been identified as the Mediterranean peninsulas of Europe (Iberia, Italy and the Balkans) with at least three main latitudinal expansion routes [4,12]. Several studies have suggested that this model is incomplete and may not explain the genetic patterns seen in many temperate species [7,8,15–19]. Therefore, other possibilities have been refined, including the existence of cryptic northern refugia [20], microrefugia [21,22], and refugia within refugia [23]. Understanding the effects of the last glacial and post-glacial period on cold-adapted species is more complex. It has been suggested that the distributions of cold-adapted species are at their minimum in the current interglacial period, and therefore, such species are now in refugia [7]. Continental refugia were also proposed by Stewart et al. [7], with some European species currently occupying eastern refugia. Hewitt [3,4] and Randi [24] earlier posited eastern refugia for temperate species that were active during glacials rather than interglacials.

The evaluation of how populations of species responded to past climate change was initially based on phylogeographic studies solely using contemporary specimens. More recently, ancient DNA (aDNA) has provided a means of testing the likely responses of species to climate changes by adding a time dimension. Carbon dating and aDNA analyses have provided further evidence of the existence of northern refugia for temperate species (e.g., [25]). Cold-adapted species have also been investigated to determine how these taxa have responded to climate warming since the last glacial period, whether by extinction and population turnovers or habitat tracking during the end-glacial/post-glacial period [26–31].

Most of the phylogeographic literature is based on single species or limited numbers of related species. Due to differences between studies (discrepancies in genetic markers, geographical areas sampled and theoretical approaches), comparative analyses have not often been attempted, with some exceptions [5,19,32–35]. It has long been noted that populations in areas that were glacial refugia should show higher genetic diversity than areas colonized by those refugia [2,3]. Thus, patterns of contemporary genetic diversity, using appropriate indices, should be a valuable general approach to infer glacial refugia. However, it is also possible to get high genetic diversity in areas of mixing from different refugia, which may occur far from the refugia [35,36]. Therefore, it is helpful that the locations of glacial refugia are expected to show a high frequency of private alleles [32,37]. Combining the approaches of comparing genetic diversity and private allele frequencies has proved insightful and helpful in identifying common phylogeographic patterns [32,35,37].

The present study aims to determine the main phylogeographic patterns of 23 terrestrial mammal species, including modern humans, by combining all available sequences of a fragment of the control region of the mtDNA for these species within Europe. We combine intra-specific and inter-specific approaches in a meta-analysis of haplotype diversity and private haplotype richness to detect potential refugia and possible common phylogeographic patterns among species.

2. Materials and Methods

For our analyses, after an initial literature search generated 225 mammal species in Europe, we limited ourselves to terrestrial mammal species, excluding bats, with a broad sample range (0.5×10^6 km^2) within Europe (SI, Supplementary Text). Due to the small sample size and peculiarities in the sequence availability, we restricted consideration to 23 species based on available data up to 2021; all had a sample size of at least 50 individuals. For those species with less than 50 sequences available, the analysis has not been conducted (SI, Supplementary Text, Tables S1 and S2).

The total number of individuals included for each taxon and the number of individuals from each geographic region varied among the studies considered for the meta-analysis. For a comparison of geographic regions, we divided Europe based on biogeographic subdivisions or discontinuities identified from previous phylogeographic and palaeoecological studies. Not assigning a coordinate to each sample is because of insufficient published information [38], and therefore, countries are defined as the minimum geographical unit in the analysis.

This ensured a minimum sample size across each region of more than five individuals for the species analyzed. These regions are represented by Iberia, Western Europe, Central Europe, Italy, the British Isles, the Balkans, Eastern Europe, Scandinavia, Caucasus, and Anatolia (SI, Figure S1). Through this delimitation, the understanding and identification of refugial areas can be addressed with confidence. This is because the main hypotheses suggested for most of the species previously analyzed were southern and northern refugia, which can be readily distinguished from our geographic subdivisions.

The most widely used measures of genetic diversity in population studies are haplotype and nucleotide diversity [39,40]. To calculate those values, we required a full reconstruction of the data sets. We calculated the number of haplotypes and haplotype (hd) diversity using DNAsp v.5.10.01 [41]. Under-sampling can affect diversity indices, as larger sample sizes tend to increase haplotype diversity [40,42]. Estimates of haplotype sampling coverage indicate how much of a population's genetic diversity is represented by a specific sample size. Achieving high sampling completeness is crucial for ensuring the accuracy of meta-analyses. As recommended by Pedreschi et al. [19], we established a minimum completeness threshold of 75%. To account for differences in the geographical distribution of samples, we employed rarefaction [43]. Specifically, to mitigate the effects of varying sample sizes on genetic diversity estimates, we used the rarefaction method in HP-RARE [44] to calculate haplotype richness and the richness of private alleles. The minimum sample size across species and regions was set according to the number of rarefied haplotypes, following Lumibao et al. [37].

Another commonly used estimation for genetic diversity is the raw number of haplotypes. To exploit private haplotypes as a means to identify refugial populations [32,45], we made use of the expectation that the haplotype frequencies should be higher than the genetic distance between haplotypes [10,35,45]. For standardization of the private allelic richness, we set a rarefaction method to a standard sample size of 10 using HP-Rare v1 [44]. We analyzed and calculated these values for each species and for each geographic region (where sufficient sequences were available) with the aim of determining commonality in patterns between species.

3. Results and Discussion

The present study used a comparative approach to study 23 wild mammal species from across Europe. The taxa studied belong to the Rodentia, Lagomorpha, Eulipotyphla, Carnivora, Primates and Artiodactyla (Table 1). Haplotype and nucleotide diversity values were calculated for each species, and each geographic region analyzed (SI, Figure S2). Rodents and Eulipotyphla show relatively consistent high values for nucleotide diversity (SI, Figure S2). This is in accordance with Pedreschi et al. [19], who revealed high genetic diversity values for small mammals in general. In carnivorans and artiodactyls, the diversity values have been found to be more variable (Figures 1 and S2), and there are species with relatively low haplotype diversity (*Lynx lynx*, *Bison bonasus*, and *Sus scrofa*). Small mammals displayed higher average haplotype diversity (mean ± s.d. = 0.94 ± 0.04) than large mammals (0.78 ± 0.17). The highest values of diversity across all mammals studied were identified in *Arvicola amphibius*, *Lepus timidus*, and *Mustela nivalis* (Figure 1).

The haplotype diversity values are displayed in Figure 1, where species are grouped by taxonomy. The results vary considerably by species and region analyzed. This reinforces the view that haplotype diversity, taken alone, provides misleading inferences for identifying refugia, even when diversity is shown on maps on a species-by-species and region-by-region basis [32]. The high haplotype diversity found, for example, across modern humans in the Palaeolithic and Mesolithic complicates any identification of possible refugia from the haplotype diversity values (Figure 1).

Table 1. Classification of mammalian species included in the analysis. Number of individuals, sequence length, and number of haplotypes.

Order	Family	Species	Common Name	Number of Individuals	Sequence Length (bp)	Number of Haplotypes
Rodentia	Cricetidae	*Arvicola amphibius*	European Water Vole	90	643	58
Rodentia	Cricetidae	*Microtus arvalis*	Common Vole	683	274	73
Rodentia	Cricetidae	*Clethrionomys glareolus*	Bank Vole	1110	250	126
Rodentia	Cricetidae	*Cricetus cricetus*	Common Hamster	561	210	44
Rodentia	Sciuridae	*Sciurus vulgaris*	Eurasian Red Squirrel	1050	249	214
Rodentia	Castoridae	*Castor fiber*	Eurasian Beaver	633	487	36
Lagomorpha	Leporidae	*Lepus europaeus*	European Brown Hare	2177	225	247
Lagomorpha	Leporidae	*Lepus timidus*	Mountain Hare	454	266	200
Eulipotyphla	Erinaceidae	*Erinaceus europaeus*	Western European Hedgehog	387	405	56
Eulipotyphla	Soricidae	*Sorex minutus*	Eurasian Pygmy Shrew	280	290	138
Carnivora	Canidae	*Canis lupus*	Grey Wolf	1613	235	35
Carnivora	Canidae	*Vulpes vulpes*	Red Fox	983	219	146
Carnivora	Mustelidae	*Mustela erminea*	Stoat	207	502	66
Carnivora	Mustelidae	*Mustela nivalis*	Least Weasel	192	514	82
Carnivora	Mustelidae	*Martes martes*	Pine Marten	705	217	77
Carnivora	Felidae	*Lynx lynx*	Eurasian Lynx	810	498	50
Carnivora	Ursidae	*Ursus arctos*	Brown Bear	849	122	141
Primates	Hominidae	*Homo sapiens*	Modern Human	86	325	35
Artiodactyla	Cervidae	*Alces alces*	Eurasian Elk	1586	465	74
Artiodactyla	Cervidae	*Capreolus capreolus*	European Roe Deer	2839	293	181
Artiodactyla	Cervidae	*Cervus elaphus*	Red Deer	4077	180	46
Artiodactyla	Bovidae	*Bison bonasus*	European Bison	172	225	25
Artiodactyla	Suidae	*Sus scrofa*	Wild Boar	1220	73	39

The results of this study underscore the complexity inherent in using genetic diversity in mtDNA to identify glacial refugia in mammals. Our findings suggest that common genetic signals are often elusive, with species-specific responses playing a crucial role in reconstructing post-glacial recolonization patterns. Although we focused on a single taxonomic group (mammals) compared to previous comparative phylogeographic studies (e.g., [4,5]), the inclusion of a large number of species with substantial sample sizes has provided a robust framework for addressing these key phylogeographic questions.

However, it is important to acknowledge that relying solely on genetic diversity for the identification of refugia presents significant challenges and potential biases. These limitations must be carefully considered in future studies. For instance, the concept of southern richness, often interpreted within the southern refugial paradigm [3,12], may represent a simplistic view and might reflect areas of endemism rather than true source populations for post-glacial recolonization of northern regions [7,15,19,20]. In this context, the allelic richness observed in mid-latitudinal regions could provide insights into the

significance of western and central European areas as "hubs of diversity" rather than merely zones of contact and hybridization.
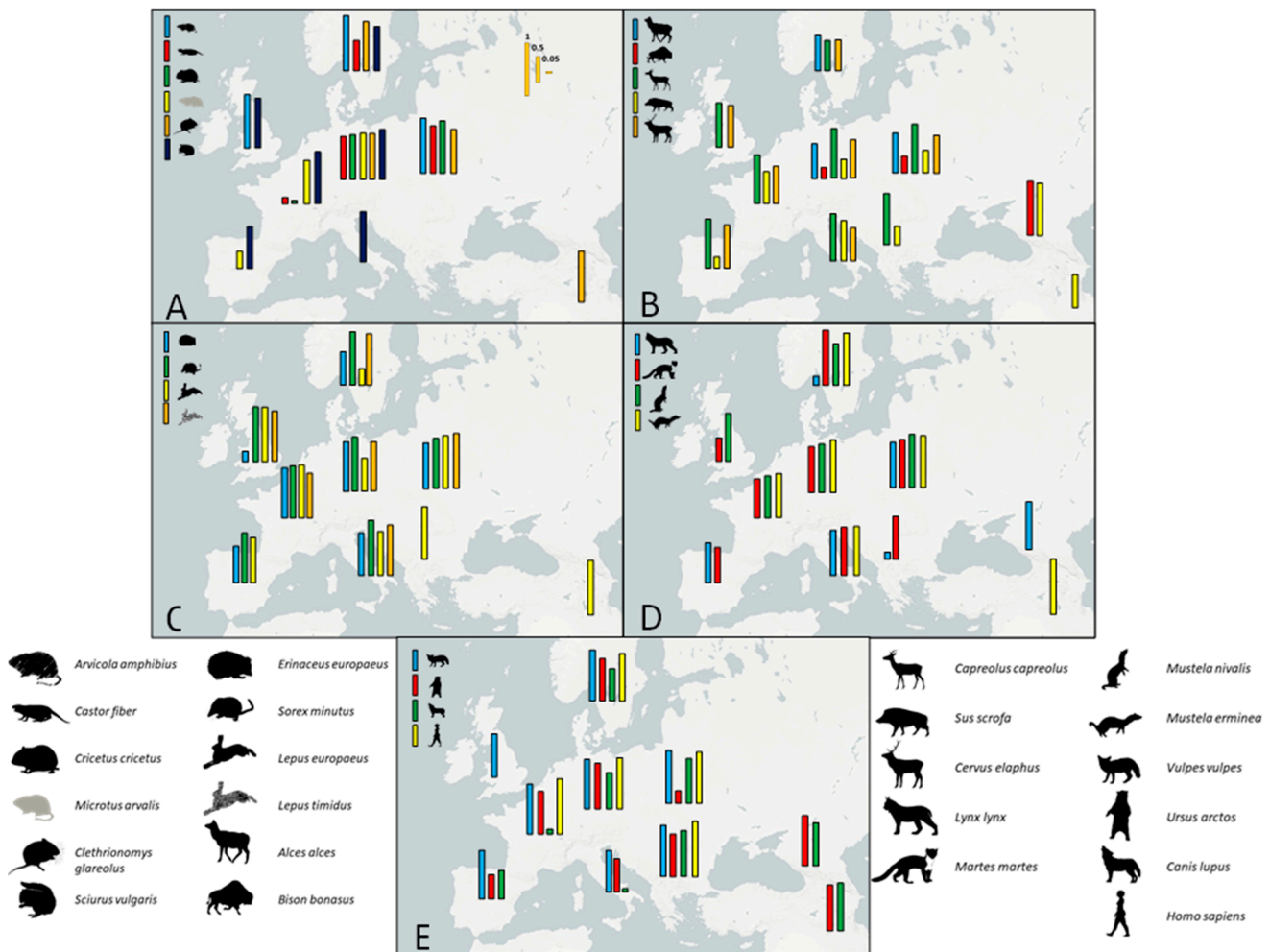

Figure 1. Maps displaying the contemporary D-loop haplotype diversities for each species among ten predefined geographic regions. (**A**) Rodentia, (**B**) Artiodactyla, (**C**) Lagomorpha and Eulipotyphla, (**D**) Carnivora (Felidae, Mustelidae), and (**E**) Carnivora (Canidae, Ursidae) and Primates. The contemporary human haplotype diversity shown is that during the Mesolithic and not modern times.

The haplotype diversity values have more value when combined with calculations of private allelic richness after rarefraction to S = 10. The values for each species by region are shown in Figure 2. Four different patterns can be inferred based on the private allelic richness values complemented with the haplotype diversity values (Figures 1 and 2). The first pattern (Figure 2A) shows an east-to-west cline with the highest values of private allelic richness in the east and the lowest in the west and is seen in *Bison bonasus*, *Alces alces*, *Lynx lynx*, *Castor fiber*, *Cricetus cricetus*, *Mustela nivalis*, and *Mustela erminea* (excluding the British Isles). This pattern is also reinforced by the haplotype diversity values found in *Castor fiber*, *Cricetus cricetus*, *Alces alces*, and *Mustela nivalis* but not for *Mustela erminea*, where the haplotype diversity values appear more homogeneous over the geographical distribution. The results for these species may reflect more than a single historical process. *Lynx lynx* and *Alces alces* include a strong association with boreal forests today [34,46], which is most prominent in northern and eastern Europe and may have had LGM refugia in the east [46]. The same may also apply to *Mustela erminea* [47]. *Cricetus cricetus* is, however, a species that is adapted to more continental steppe habitats [48] and may well have contracted since the LGM only to re-expand during the Neolithic as cereal cultivation spread west across Europe, as has been suggested for the common vole (*Microtus arvalis*) [49]. *Cricetus cricetus*

would otherwise be in an Eastern refugium today [7]. In *Castor fiber*, *Mustela nivalis*, and *Bison bonasus*, the situation is more complex due to the substantial reduction of populations and the low diversity in recent times seen in *Bison bonasus* and *Castor fiber* [50,51] and uncertainty about the subspecies affinities of different populations previously described in *Mustela nivalis* [52].
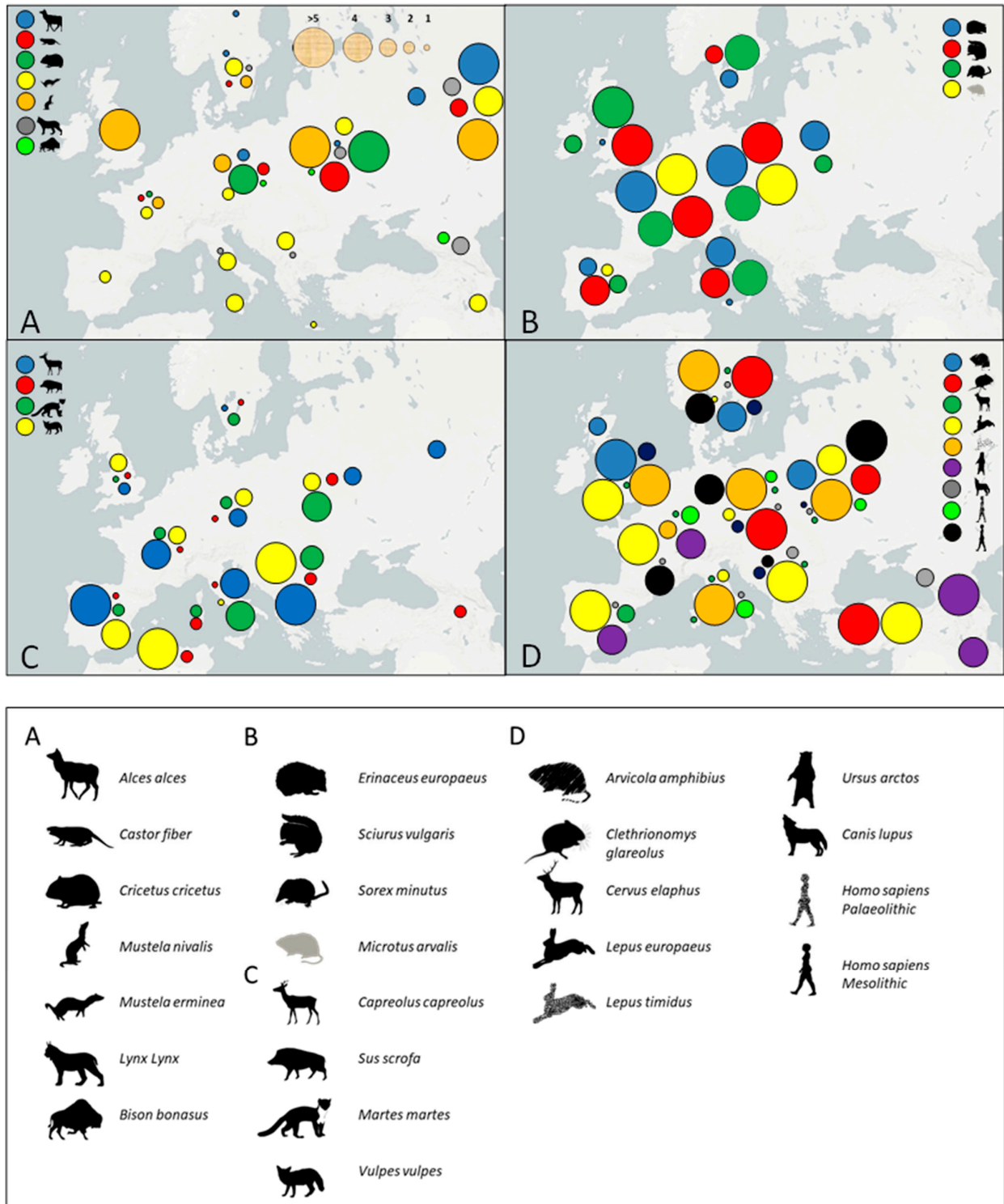
Figure 2. Maps displaying the four main patterns of distribution identified for private allelic richness identified after rarefaction to S = 10. (**A**) East–west decline in variation; (**B**) Western-Central belt of highest diversity; (**C**) Southern richness; and (**D**) Homogeneous with no geographic pattern.

The second pattern identified (Figure 2B) relates to a Western-Central belt that comprises the highest values of private allelic richness for *Erinaceus europaeus*, *Sciurus vulgaris*, *Sorex minutus*, and *Microtus arvalis*. It is interesting that the species showing this second pattern are all small mammals, suggesting some association with low dispersal rates, although not all small mammals conform to the pattern. *Erinaceus europaeus* and *Microtus arvalis* have a similar haplotype diversity pattern as found with private alleles [53], although that was not the case for *Sciurus vulgaris* and *Sorex minutus*, further emphasizing species-by-species variation [54] (Figure 1). Although haplotype diversity did not reveal a pattern for the red squirrel (*Sciurus vulgaris*), private allelic richness indicates Western and Central Europe as possible refugial areas for the species. For *Sorex minutus*, the pattern is not as clear as for the other species and the high values for private allelic richness identified in the whole range of the species complicate the resolution. However, the importance of areas in France as possible refugia has been suggested [55], which is consistent with the results here. Therefore, these species may be the ones that were in cryptic northern refugia during the LGM in Europe, as has been previously suggested [20,56,57].

The third pattern (Figure 2C) is one where the greatest diversity is in the south of Europe. *Capreolus capreolus*, *Sus scrofa*, *Martes martes*, and *Vulpes vulpes* display this pattern of high private allelic richness in the south (east and west) and low values in northern latitudes. *Capreolus capreolus*, *Sus scrofa*, and *Martes martes* appear to have had southern refugia apparently coupled with complex demographic histories. The human actions of the introduction of domestic pigs, conspecific with wild boar (*Sus scrofa*), and the translocation of roe deer (*Capreolus capreolus*) may have affected the genetics of these species [58–60], although our analyses have not detected that. A previously described lack of phylogeographic structure and homogeneous distribution in the red fox (*Vulpes vulpes*), suggested that there may have been a constant occupation of the region by this species [61]. In contrast, the results here show *Vulpes vulpes* to have a southern refugial pattern where Iberia, and especially the Balkans, represent important areas for private allelic richness. The pattern observed here for *Vulpes vulpes* is in accordance with the recent study from McDevitt et al. [62]. Overall, the pattern of southern richness in diversity accords with species that resided in southern refugia during the LGM, conforming to the traditional scenario for European species [12,13].

The homogeneity in genetic variation identified in some species, the fourth pattern, suggests there is no clear, structured pattern of distribution of private alleles (Figure 2D). This is superficially similar to that of the northern refugium pattern; however, the distinction is seen in the results for each individual species (Figure 2). This is in accordance with the findings of Hofreiter et al. [63] for the Late Pleistocene genetic landscape but extended to the present day. For eight different species, a homogeneous distribution of private alleles was found, and areas with much higher diversity than others were not identified (Figures 1 and 2). Modern humans from the Palaeolithic and the Mesolithic are amongst the species with this pattern.

The body size of a species does not appear to be associated with a homogeneous distribution of private alleles, as four of the species displaying this are small mammals (*Arvicola amphibius*, *Clethrionomys glareolus*, *Lepus europaeus*, and *Lepus timidus*), and four are large (*Cervus elaphus*, *Canis lupus*, *Ursus arctos*, and *Homo sapiens*). In general, these species are characterized by a widespread range and homogeneous distribution, and a relative lack of ecological restrictions may help explain this private allele distribution. The absence of phylogeographic patterns in some species has been explained by their high migration rate, such as *Canis lupus* [64]. It is interesting to note that two of these species (water vole *Arvicola amphibius* and brown bear *Ursus arctos*) were described by Hewitt [3,4] as having had southern refugia exclusively. The latter has been shown to be incorrect for the brown bear and has been questioned for *Arvicola amphibius*, as well as *Cervus elaphus*, based on aDNA and other studies [65–68]. The Spanish brown bear haplotype of Hewitt [4] has been found in Belgium during the LGM, and the red deer and water vole are represented on either side of the LGM by the same populations in northern Europe. These data may be

consistent with the homogeneity described here. *Cervus elaphus* should perhaps be regarded with some caution as they are known to have been translocated in historical times, which may have homogenized their geographic pattern of diversity [68]. Kotlík et al. [36], on the other hand, have inferred that *Clethrionomys glareolus* had cryptic northern refugia as well as southern refugia—and this might be another explanation for the pattern described here. *Homo sapiens* populations from the Palaeolithic as well as the Mesolithic do not show any strong pattern, with only a slightly higher observed occurrence of private alleles in the west during the Mesolithic. In general, the private allelic richness is higher in the Mesolithic than the Palaeolithic, either indicating fragmentation of populations in the continent during the LGM and/or major re-expansions [69,70], leading to an increased number of regionally private haplotypes.

The four disparate phylogeographic patterns identified here are likely to be dominantly influenced by the historical biogeography of the individual component species and their constituent populations. The general explanation for such patterns is that the species' populations were restricted to refugia during the adverse conditions of the last glacial maximum, followed by a re-expansion during the Holocene [3,4]. While it is likely that the most recent dramatic climate changes have affected these species, it is also possible that some geographic patterns have an older legacy. It should be kept in mind that the Milankovitch glacial/interglacial cycles have affected taxa during the entirety of the Quaternary.

The four patterns identified include two that correspond to a refugial source recognized by Hewitt [3,4], namely the southern and eastern refugia, although, since that time, there has been greater acceptance of the third pattern, the extra-Mediterranean northern refugia [24]. The taxa that had a Western-Central diversity increase may represent species that had cryptic northern refugia, and all are relatively small species that have previously had such claims [20,56]. It should be noted, however, that for *Sorex minutus*, Vega et al. [71] (and previous studies referenced therein) posit southern refugia in addition to the northern refugia that we have highlighted thus far—a similar situation as for the other species with Western-Central diversity [14,53,54]. However, the signal of refugia, in terms of the presence of private alleles, is stronger for the northern refugia. The species with an apparent lack of pattern are ones that have not previously been widely recognized and indicate species that either had a panmictic distribution during the LGM or had refugia both in the Mediterranean and in the extra-Mediterranean region (with an equally strong signal for refugia in the southern and northern refugia). Interestingly, these taxa include several (the water vole and the brown bear) that had been identified by Hewitt [3,4] as having had southern LGM refugia. Furthermore, some of these had also led to the suggestion of cryptic northern refugia, namely *Cervus elaphus* and *Arvicola amphibius* [66,67] and *Ursus arctos* was also implicated in a model for the evolution of *Ursus maritimus* in a cryptic maritime northern refugium [69]. The idea that *Ursus arctos* had been in one or more cryptic northern refugium could be interpreted from the work of Ersmark et al. [65], although this had not been specifically claimed by them (they used the more general phrase, "northern survival"). This may suggest that the concept of cryptic northern refugia may have been overstated and that some of the species proposed as having had such refugia had instead panmictic populations. The alternative is that some or all of these species had both northern and southern refugia, as has been proposed for the bank vole [36].

A possibility is that the more dispersive larger mammals like *Canis lupus* and *Homo sapiens* were panmictic while the smaller mammals had more isolated northern and southern refugia. Both archaeological [72] and whole mtDNA and whole-genome aDNA data [73,74] suggest that southwest Europe served as a human refuge during the LGM and that there was substantial genetic turnover in Europe between 25,000 and 11,500 years ago but with the continuity from the Aurignacian to the Magdalenian and the Solutrean followed by new ancestries spreading from a likely refuge in the southeast after 14,500 years ago [75–77]. Nevertheless, the pattern is complex, and in our analyses, modern humans from the Palaeolithic and the Mesolithic conform to the lack of phylogeographic structure, indicating that contrary to some suggestions [69,78], they were not restricted to a southern refugium

during the LGM [70,79]. Some of the other mammalian species with a lack of pattern for private allele richness may be similar to birds in the Palaearctic, for whom it was suggested there had been panmixia during the LGM [80]. The lack of pattern is interesting because this may be viewed as a negative result and/or suffer from publication bias. Negative results are often difficult to publish [81], which can lead to non-representative perceptions.

4. Conclusions

The species-specific analysis of the 23 mammals investigated here has identified a number of patterns in the diversity of mitochondrial D-loop sequences. This meta-analysis is unusually rich in terms of the number of species using the same genetic marker and contributes to a better understanding of mammalian phylogeography in Europe specifically and the complexity of biogeographical processes more widely.

A new approach to locating potential refugial areas in the continent has been established based on identifying areas where private allelic richness displayed high values and was complemented by haplotype diversity indices. This research builds on the legacy of the comparative approach [5,13,32,35], although it provides a novel method to recognize similarities between species.

A weakness of the analysis performed here is that it does not take into account the phylogenetic distribution of genetic lineages. In the future, when it becomes possible for taxa with good sampling, it would be beneficial to study diversity and private allele distribution on a lineage-by-lineage basis. It would also be of interest to see a replication of the meta-analysis with whole mitochondrial genomes, and indeed whole genomes, on large numbers of specimens over large areas to interpret phylogeography. It is also desirable to analyze numerous samples over time using DNA analysis. Such approaches would help identify confounding factors, such as recent bottlenecking, but have as yet only been possible for a few taxa.

Four different patterns are revealed, consisting of species that have an east-west decline in variation, ones with a Western-Central belt of highest diversity, another with southern richness, and finally, a pattern of homogeneity where no geographic pattern was identified. These patterns would seem to reflect the refugial origins (or lack thereof) of the modern populations. The east–west cline appears to mostly describe the species with eastern refugia during the LGM, albeit differing ones according to the adaptations of the species, and the southern richness pattern seems to correspond to species with southern European refugia. These were the two patterns that had been described by Hewitt [3,4] and Randi [24]. However, one of the species (*Cricetus cricetus*) may correspond to a continental species that is actually in a refugium today [7], although it may have expanded westwards during the Neolithic in response to anthropogenic changes in the landscape. The species with Western-Central belt richness may describe species that had been in cryptic northern refugia [20]. Finally, the species with a more homogeneous pattern may have been widely distributed in the mid-latitudes of Europe during the LGM and effectively had a large refugium at the time or could be described as having no refugia, or they were located in separate refugia both in the northern extra-Mediterranean as well as Mediterranean areas [36].

The homogeneous pattern seen in some species suggests that large taxa like the brown bear had not been in a southern or a cryptic northern refugium but were widely distributed at the time of the LGM in the European mid-latitudes. The latter may suggest that the concept of cryptic northern refugia may have been overstated and that some of the species proposed as having had such refugia had instead panmictic populations. It may be, however, that other, especially smaller, mammalian taxa, such as the bank vole, had isolated refugia in the south and the north, although distinguishing between these explanations for the homogeneous patterns may be challenging. In conclusion, the meta-analysis of existing phylogeographic data has suggested that four patterns exist: species with eastern, northern and southern refugia, as well as mammals that may not have substantially contracted over non-glaciated areas during the LGM.

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